

## 4. *Nothofagus* and its parasites: a cladistic approach to coevolution

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### Abstract

Cladistics is the discipline that hypothesizes genealogical relationships among taxa. In this paper we use parsimony methods to find the shortest possible sequence (principle of parsimony) of grouping character states (synapomorphies), to compare the phylogenies of the contemporary host species of *Nothofagus* (Fagales) and the species of three groups of contemporary parasites, *Heterobathmia* (Lepidoptera), Eriococcidae (Hemiptera), and *Cyttaria* (Cytariales) which live on them. We consider two general questions. Firstly, do hosts and parasites share a common history of 'association by descent' (coevolution) or have parasites become parasitic through colonization. Secondly, we ask whether coevolution is a by-product of biogeography.

### Introduction: parasitism by 'association by descent' and 'colonization'

Mitter and Brooks (1983) pointed out that the idea of coevolution by 'association by descent' is an old one (e.g. Kellog 1896). Examples from

a variety of parasitological studies between hosts and parasites abound, especially internal parasites of fishes and tetrapods, and fungi on plants and animals. Among plants the southern beeches of *Nothofagus* are parasitized by a wide variety of different groups including insects, (e.g. moths, psyllids, coccids, and aphids), fungi, and some mistletoes. Schlinger (1974) gives a remarkable narrative with an example of an intricate phytophagous insect–primary parasitoid insect–hyperparasitoid insect interaction for *Nothofagus*, involving the phytophagous aphids *Neuquenaphis* and *Sensoriaphis*, their primary parasites *Pseudephedrus* and *Paraphedrus*, respectively, and their secondary parasites *Alloxysta*.

The concept that the systematic and biogeographic patterns of hosts might be more positively elucidated by looking at their specific parasites was articulated clearly by Metcalf (1920, 1929) who studied leptodactylid frogs and their opalinid parasites. Science proceeds with formal characterizations of problems and Eichler (1941) began to formalize Metcalf's ideas with 'Fahrenholz's rule' (see Mitter and Brooks 1983) which states that: 'in the case of permanent parasitism the relationship of the host can usually be inferred from the systematics of the parasites'. Hennig (1966) pointed out, however, that most studies utilizing this concept were based not on genealogies, but 'affinities'. Despite the detailed studies of Schlinger (1974) on the *Nothofagus* aphids and their parasites, where he acknowledges the importance of phylogenetic taxonomy, and those of Korf (1983) on the phylogeny of the parasitic *Cyttaria* fungi, both authors derive their coevolutionary theories from the *Nothofagus* phylogeny rather than using independent phylogenies and comparisons of the parasites and hosts.

We intend to extend beyond Fahrenholz's rule by using independent cladistic studies of three parasite groups, the moths of *Heterobathmia*, the scale insects of Eriococcidae, and the fungi of *Cyttaria* on their *Nothofagus* hosts. We try to see to what extent equivalent components occur in the hosts and their parasites rather than having one dependent on the other.

### 1. Cladistics: the method and an algorithm

Phylogenetic patterns are best represented by a branching diagram, a cladogram (Fig. 4.1). The tips or terminals (e.g. A, B, C, D, or 1, 2, 3, 4) represent the individual taxa from which the character data have been sampled. The nodes or branch points are determined by character state distributions (e.g. Fig. 1a–c). The character state polarities within each group are usually determined by comparison to an outgroup, a related group which may or may not be the sister group to the study group. One purpose of cladistics is to recognize monophyletic groups which for us are determined by proposing cladograms that have the

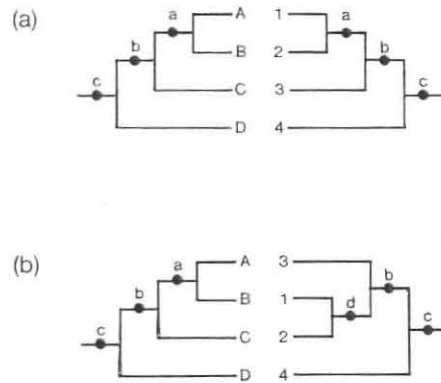


Fig. 4.1. Hypothetical phylogenies of a host group (A-D) and its parasites (1-4). (a) Exact correspondence between the host and parasite cladograms each showing the same components a, b and c. (b) Partial correspondence between the host and parasite cladograms each sharing two common components, b and c, and two unique components, a and d.

simplest (most parsimonious) distributions of character state changes over the taxa, i.e. the fewest number of proposed character state changes. For a fully dichotomized cladogram with  $n$  taxa there are  $n-1$  nodes. The smallest number of changes for a specified characteristic is one less than the number of character states, i.e. a single origin for each state on the tree (Mitter and Brooks 1983). When a particular state is found in all and only the members of a putative monophyletic group, then we can propose that the character state evolved once and only once. In the general sense Hennig (1966) said that any group of taxa composed of all the descendents of a single ancestor, and only those descendents, is monophyletic, a definition which can be justified empirically by saying that monophyletic groups are due to common ancestry and homologous characters distinguish monophyletic groups (see Patterson 1982). For a more detailed discussion of cladistics with reference to the application of parsimony and an appraisal of homology see Humphries and Funk (1984).

In estimating a phylogeny for a particular group it is necessary to select one cladogram from a multitude of others. Most taxonomists are not aware of how many there are for a given number of taxa (Felsenstein 1978). For bifurcating rooted cladograms there are 3 for 3 taxa, 105 for 5 and 34459425 for 10! The computational problem is now simplified by several computer programs (see Luckow and Pimentel 1985). Those incorporating the Wagner algorithm (Farris 1970) or the branch and bound algorithm (Hendy and Penny 1982) are perhaps the most effective since they are both consistent with the parsimony criterion for minimizing

the number of character state changes during analysis. Both algorithms find the cladogram of minimum length, the most parsimonious one from a given set of information (see Kluge and Farris 1969; Farris 1970). We used PAUP (Phylogenetic Analysis Using Parsimony), an interactive Fortran 77 program for inferring phylogenies under maximum parsimony (Swofford 1984). PAUP allows a choice of optimization procedures (accelerated transformations, delayed transformations, and Farris optimization), it holds equally parsimonious cladograms in memory, has branch-swapping routines and can handle ordered versus unordered character transformations, missing characters, and large data matrices. The computer printouts are kept at the British Museum (Natural History).

## 2. *Components, coevolution and colonization*

In comparing two independent phylogenetic hypotheses such as that of a parasite and that of its host we require a method based on the original empirical observations; the character data. Component analysis is one way this may be done (Nelson and Platnick 1981). In Fig. 4.1 the letters A–D refer to the host taxa in a host phylogeny and the numbers at the terminals refer to taxa of two different parasite phylogenies. The characters upon which each of the three phylogenies have been based can be substituted with letters a, b, c . . . etc. to define similar components. In Fig 4.1a complete correspondence between host and parasite is represented by the fact that components a–c, effectively hypothetical ancestors in this case, are common to both groups. The most defensible hypothesis, assuming the cladograms are equivalent to the actual host and parasite phylogenies, is that the ancestors of the groups A, B, C, D, and 1, 2, 3, 4 speciated at node 'C' to give two taxa for each group the ancestor of A, B, C, and D in the host, and 1, 2, 3, and 4 in the parasite. A second speciation event at node 'b' gave the ancestor of A, B, and C and 1, 2, and 3. The most parsimonious hypothesis explaining the exact correspondence between host and parasite is that speciation events occurred simultaneously (Mitter and Brooks 1983).

In Fig. 4.1b, the speciation events in common are represented by components 'b' and 'c', suggesting a partially shared history. However, non-correspondence between components 'a' and 'd' can only be explained by *ad hoc* hypotheses. If the host phylogeny is assumed to be 'correct', then the alternative component 'd' in the parasite phylogeny requires explanation. One possibility is that parasitism by colonization occurred; either species B was invaded by parasite 2 from C which then speciated or that species C was invaded by parasite 1 from B which subsequently speciated. Alternatively, 'association by descent' predicts

that the lineage isolating species C in the host should be older than the lineage to the one from node 'a' to species A. To reconcile the expectation with the apparent reversal of the position for parasite 2 we have to postulate a sequence like that given in Fig. 4.2. The independent derivation of parasite 1, and the ancestors of 2 and 3 from a similar origin requires that parasite 1 now found on A must have either failed to parasitize B and C, or have become extinct upon them. Similarly, to account for a common ancestry of parasites 2 and 3 requires a similar failure of parasitism or extinction of a parasite on A. The net result is that there are now six speciation events, instead of three, required to explain the present-day pattern of evolution as 'association by descent'.

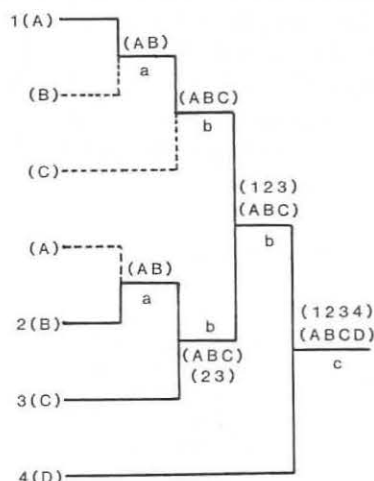


Fig. 4.2. Hypothetical history for the parasite group given in Fig. 4.1. (b). Dotted lines represent lineages failing to be parasitized, or losing parasites (extinction) — the hosts, parasites, and their ancestors are represented at the tips and nodes as upper case letters and numbers and equivalent components in lower case letters.

Interpreting cladograms as successive speciation events at the nodes makes predictions about the sequence or history of parasitism that is based on a character analysis of the parasites themselves. As Mitter and Brooks (1983) point out there is an obvious resemblance between 'association by descent' versus 'colonization' in historical parasitism with 'vicariance' versus 'dispersal' events in historical biogeography. Parasites occur in hosts either because they speciated at the same time for the same reasons or because they invaded from another source. Geographical disjunctions between related taxa showing similar patterns to unrelated taxa are hypothesized as occurring simultaneously and a result of historical, geographical, or ecological events. Non-correspondence

between groups occurring in the same areas invites *ad hoc* explanations of which dispersals and extinctions are two.

### 3. Correspondence between host and parasite

When comparing host with parasite phylogenies it is difficult to test any hypothesis other than one of 'association by descent'. Hypotheses based on extinctions, invasion by colonization, and also host switching, all require *ad hoc* explanations because they are not based on any empirical scheme of either the host or parasite relationships. Hypotheses based on 'association by descent' predict the least number of character changes or speciation events and thus can easily be tested by new data (Mitter and Brooks 1983). In the examples to be considered here, there is a degree of discordance in the phylogenetic hypotheses of hosts when compared to those of the parasites. This is for various reasons. For example, there can be several, equally parsimonious, phylogenetic solutions for a given set of data. Secondly, there are overlapping parasite distributions, in *Nothofagus betuloides* for example (see p. 66), which have phylogenetic connections in different directions. Thirdly, not all host species within one monophyletic group are parasitized by an equal number of typo-pathogens. The method

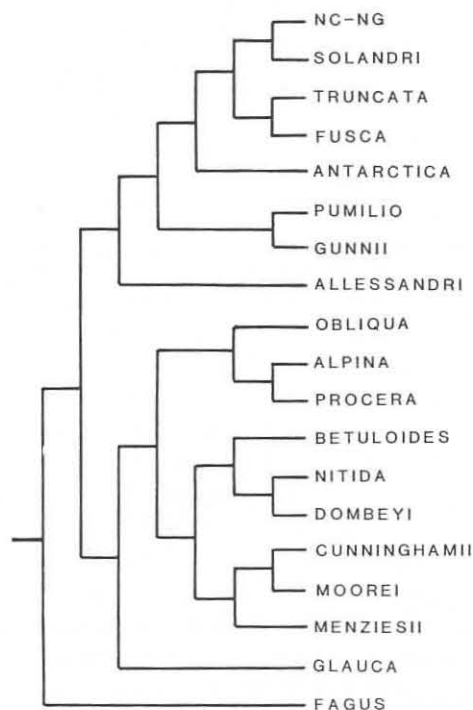


Fig. 4.3. *Nothofagus* cladogram (tree no. 40) rooted with the sister group *Fagus*. See text.

adopted here is to compare all of the available topologies generated by Swofford's PAUP program for the hosts with those of the parasites. The criterion of choice is that combination which maximized the number of common components and minimized the number of colonizations or extinctions under a hypothesis that coevolution occurs by 'association by descent'. Admittedly, this gives an *a priori* bias towards coevolution, but has the merit of choosing a result in terms of explanatory power.

### *Nothofagus*: the host phylogeny

The genus *Nothofagus* comprises about 35 species (Humphries 1981, 1983) which occur in New Guinea, New Caledonia, New Zealand, Tasmania, southern and eastern Australia, and in Pacific South America in Chile and Argentina. Here, we concentrate on those 17 species in South America, Australia, Tasmania, and New Zealand which are included in the subsections *Antarcticae*, *Pumilae*, *Quadripartite*, and *Tripartite* of van Steenis (1953, 1971) (see Figs 4.3 and 4.4). The analyses presented here are new, based on 32 characters (e.g. Philipson and

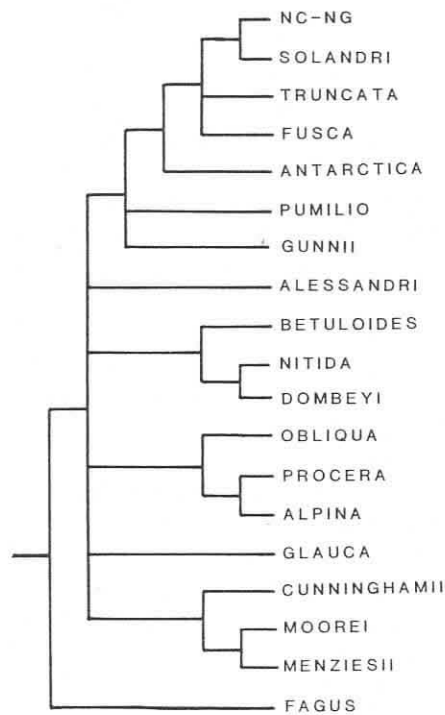


Fig. 4.4. Nelson consensus tree for all *Nothofagus* trees. See text for explanation.

Philipson 1979) and new interpretations of character transformations in the light of recent criticisms (Heads 1985; Humphries 1985). One-hundred-and-ninety equally parsimonious trees were generated with a consistency of 0.761. The cladogram which showed maximal fit with the parasite groups is given in Fig. 4.3, and to show that the topologies varied only because of zero branch lengths and alternative basal positions for plesiomorphic taxa, a Nelson consensus tree is given in Fig. 4.4 (see Nelson and Platnick 1981; Myamoto 1985).

### The parasites

#### 1. *Heterobathmia*

The genus *Heterobathmia* is the sole member group of the lepidopteran suborder Heterobathmiidna and is the sister group to all proboscis-bearing Lepidoptera, the Glossata (Kristensen and Nielsen 1983). Species of *Heterobathmia* are univoltine (i.e. with one generation per season), and the adults fly during late winter and early spring. The adult activity periods are closely correlated with the leafing and flowering of the deciduous *Nothofagus*. The larvae are leaf miners in newly set leaves of *Nothofagus* and development is rapid. After 10 days mature larvae burrow into the soil to 8–15 cm where they diapause through summer, autumn, and most of winter in a strong cocoon. The pharate adults tunnel up through the soil to the dry litter where the pupal cuticles are shed (Kristensen and Nielsen 1983).

There are 10 species, only two of which have been named, *H. pseuderiocrania* and *H. diffusa* (Kristensen and Nielsen 1979).

The data matrix was small enough to utilize the exhaustive branch and bound option in PAUP. The analysis yielded three equally parsimonious trees. Because the trees differed only in the topologies relating to the species group C, F, and G, all feeding on *N. obliqua*, and with basal zero branch lengths only the consensus tree is given (Fig. 4.5).

A reduced cladogram (Fig. 4.6) shows that the terminal sister species pair 'A' and 'B' occur in *N. antarctica* and *N. pumilio*, respectively, implying that the relationships of their hosts is *N. antarctica* sister to *N. pumilio* and those together sister to *N. obliqua*.

A comparison of this cladogram with the *Nothofagus* cladograms and consensus tree indicates that the heterobathmid moths show no direct correspondence with any of the *Nothofagus* phylogenies. At the species level an hypothesis of 'association by descent' would involve many more extinctions or failures to colonize during the *Nothofagus* phylogeny. More likely is opportunism by the sister species pair to colonize *N. antarctica* and *N. pumilio* from an origin on *N. obliqua*.



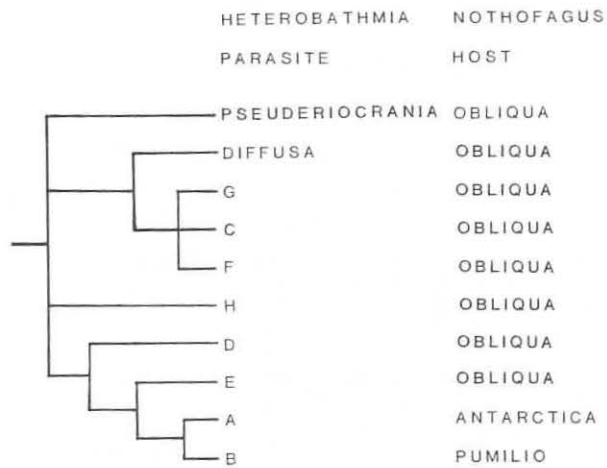


Fig. 4.5. Consensus tree for ten species of *Heterobathmia*.



Fig. 4.6. A comparison of the implied host relationship derived from the *Heterobathmia* consensus tree (see Fig. 4.5) with a simplified expression of the host cladogram (see Fig. 4.3).

## 2. Eriococcidae

The Eriococcidae are a family of scale insects (Homoptera: Coccoidea), a group in which the largely sedentary females feed on the sap of host plants. Many scale insects cause damage to the host not only by depletion of sap, but also indirectly by the transmission of viruses, the injection of toxins, and contamination by honeydew. Although the species that have been placed in the Eriococcidae probably do not form a monophyletic group, certain genera, parts of genera, or groups of genera do appear to be monophyletic. The 22 species discussed here belong to the genera *Eriococcus* and *Madarococcus*. *Eriococcus* (all species of which may not form a monophyletic group) occurs throughout the world on a wide variety of hosts. *Madarococcus* was erected for a few New Zealand species, and differs from *Eriococcus* by only a single character. All species of the Eriococcidae with spatulate suranal setae belong to one of these two genera, and all appear to be confined to *Nothofagus*. The PAUP analysis yielded more than 100 cladograms with a consistency of 0.394. However, there were only three basic topologies varying in terms of the position of *Eriococcus rubrifagi*, *E. fagicorticis*, *E. rotundus*, and *E. maskelli*.

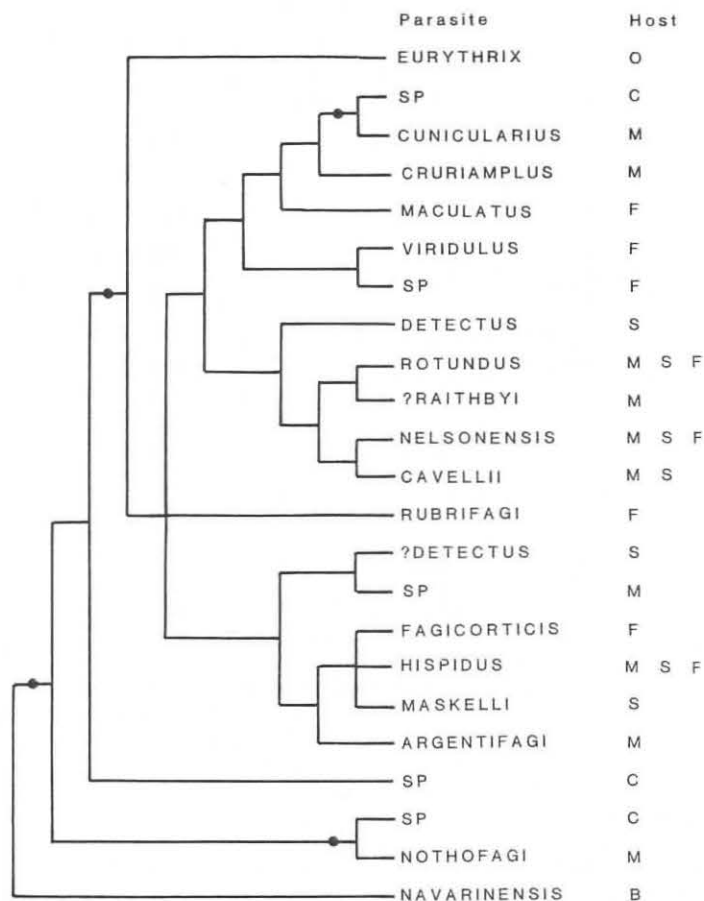


Fig. 4.7. Eriococcidae consensus tree for 22 species. B, *Nothofagus betuloides*; C, *N. cunninghamii*; F, *N. fusca*; M, *N. menziesii*; O, *N. obliqua*; S, *N. solandri*.

Because the different positions did not really affect the comparisons to *Nothofagus*, a Nelson consensus tree is given (Fig. 4.7).

A comparison of this consensus tree with the *Nothofagus* cladogram (Fig. 4.3) suggests that there are two groups of eriococcids with similar and fairly obvious correspondence with *Nothofagus cunninghamii* and *Nothofagus menziesii*, some general support for the relationship of *Eriococcus eurythrix* with New Zealand and Australian taxa, and generally the outgroup/sister group is South American (Fig. 4.8). However, at the species level the promiscuous distribution of *E. rotundus*, *E. nelsonensis* and *E. hispidus* on *Nothofagus fusca*, *N. menziesii* and *N. solandri*, together with the host-implied sister group relationships of *N. menziesii* with *N. solandri*, and *N. fusca* with *N. menziesii* and *N. cunninghamii*, suggest

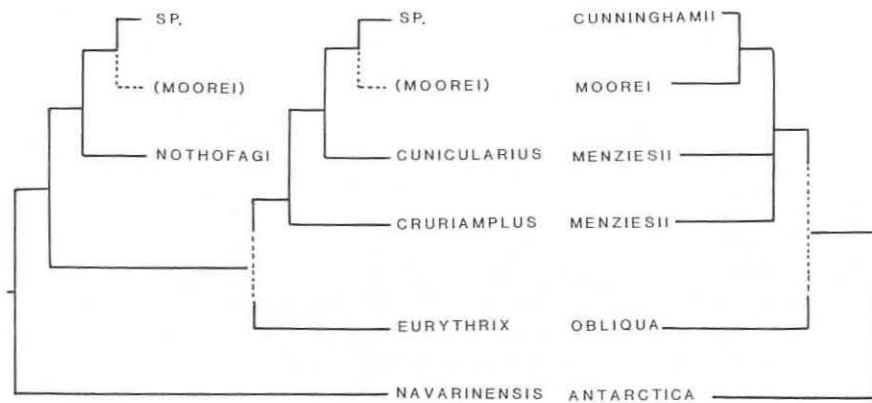


Fig. 4.8. Comparison of Eriococcidae consensus tree (see Fig. 4.7) with host *Nothofagus* cladogram (see Fig. 4.3). See text for explanation.

that, for New Zealand at least, an hypothesis of 'association by descent' would be highly unlikely. Nevertheless, the phylogenies of the two sister species pairs, *Eriococcus* sp. on *N. cunninghamii* and *E. nothofagi* on *N. menziesii*, together with *Eriococcus* sp. on *N. cunninghamii* and *Madarococcus cunicularius* on *N. menziesii* are too similar to the host phylogenies to be due to chance. Comparison to the *Nothofagus* cladograms shows that the sequence for *E. eurythrix* on *N. obliqua* and *E. naverinensis*, the outgroup species, on *N. antarctica* follows a general biogeographical pattern (Fig. 4.8).

### 3. *Cyttaria*

*Cyttaria* is a genus of eleven gall-forming parasitic fungi known only from branches and smaller twigs of twelve southern temperate species of *Nothofagus*. The pattern of pathogenicity is complicated because some species occur on one host whilst others occur on two or more; *C. hariotii* occurs on five different hosts (Table 4.1). The taxonomy of the species has been well worked out (see Santesson 1945; Rawlings 1956; Kobayashi 1966; Gamundí 1971), but studies on species interrelationships are few (Rawlings 1956; Kobayashi 1966; Korf 1983). Rawlings (1956) divided the group into two—those species with globose stromata versus those with longitudinal stromata (see Fig. 4.13a). Korf (1983) advanced a phylogeny on the principle that 'fungi are accurate taxonomists'. He recognized three groups (see Fig. 4.13c) based on geographical position, host range, and the infrageneric groups of the host as suggested by pollen types.

To make an independent analysis we used 30 characters derived from the systematic papers cited above. Two analyses using PAUP were

Table 4.1. *Cyttaria* species and hosts

Species	Hosts
<i>C. nigra</i>	<i>N. menziesii</i>
<i>C. pallida</i>	<i>N. menziesii</i>
<i>C. gunnii</i>	<i>N. menziesii</i> , <i>N. solandri</i> (incl. <i>N. cliffortioides</i> )
<i>C. septentrionalis</i>	<i>N. moorei</i>
<i>C. hookeri</i>	<i>N. antarctica</i> , <i>N. betuloides</i> , <i>N. pumilio</i>
<i>C. berteroi</i>	<i>N. glauca</i> , <i>N. obliqua</i>
<i>C. darwinii</i>	<i>N. antarctica</i> , <i>N. betuloides</i> , <i>N. pumilio</i>
<i>C. hariatii</i>	<i>N. antarctica</i> , <i>N. betuloides</i> , <i>N. dombeyi</i> , <i>N. nitida</i> , <i>N. pumilio</i>
<i>C. espinosae</i>	<i>N. obliqua</i> , <i>N. procera</i>
<i>C. jahowii</i>	<i>N. betuloides</i> , <i>N. dombeyi</i>
<i>C. exigua</i>	<i>N. betuloides</i>

undertaken, the first scoring character 2 as longitudinal for *Cyttaria jahowii*, the second treating the same character in the same taxon as unknown. The chosen outgroup, Boedijnopezizeae (Korf 1983; pers comm.), seemed only to define *Cyttaria* as a natural group. The first analysis gave 19 cladograms with a consistency of 0.56, the second 57 cladograms with a consistency of 0.59. Every cladogram was compared with every *Nothofagus* cladogram. Those showing the greatest number of components and least number of proposed colonizations to make the remaining data fit are shown (Table 4.2, Figs 4.9 and 4.10).

Table 4.2. The number of components common to three *Cyttaria* cladograms and the *Nothofagus* cladogram (40) in Fig. 4.3.

<i>Cyttaria</i> cladogram (analysis in parenthesis)	Number of common components	Postulated colonizations	Number of colonizations
19 (1)	10	1-7	7 (Fig. 9)
12 (1)	7	1-7	7
40 (2)	9	1,2,7	3 (Fig. 10)

Colonizations: 1, *C. hookeri* on to *N. pumilio*; 2, *C. hookeri* on to *N. antarctica*; 3, *C. darwinii* on to *N. pumilio*; 4, *C. hariatii* on to *N. pumilio*; 5, *C. darwinii* on to *N. antarctica*; 6, *C. hariatii* on to *N. antarctica*; 7, *C. gunnii* on to *N. solandri*.

None of the cladograms showed a 100 per cent fit without postulating some parasitism by colonization. In Fig. 4.9, the *Cyttaria* cladogram (no. 19) from the first analysis shows 10 components in common with 7 of those in *Nothofagus*. However, to make such a fit it is necessary to postulate seven colonizations for four of the *Cyttaria* species; Fig. 4.10 is a cladogram which is the best fit. It minimizes the number of

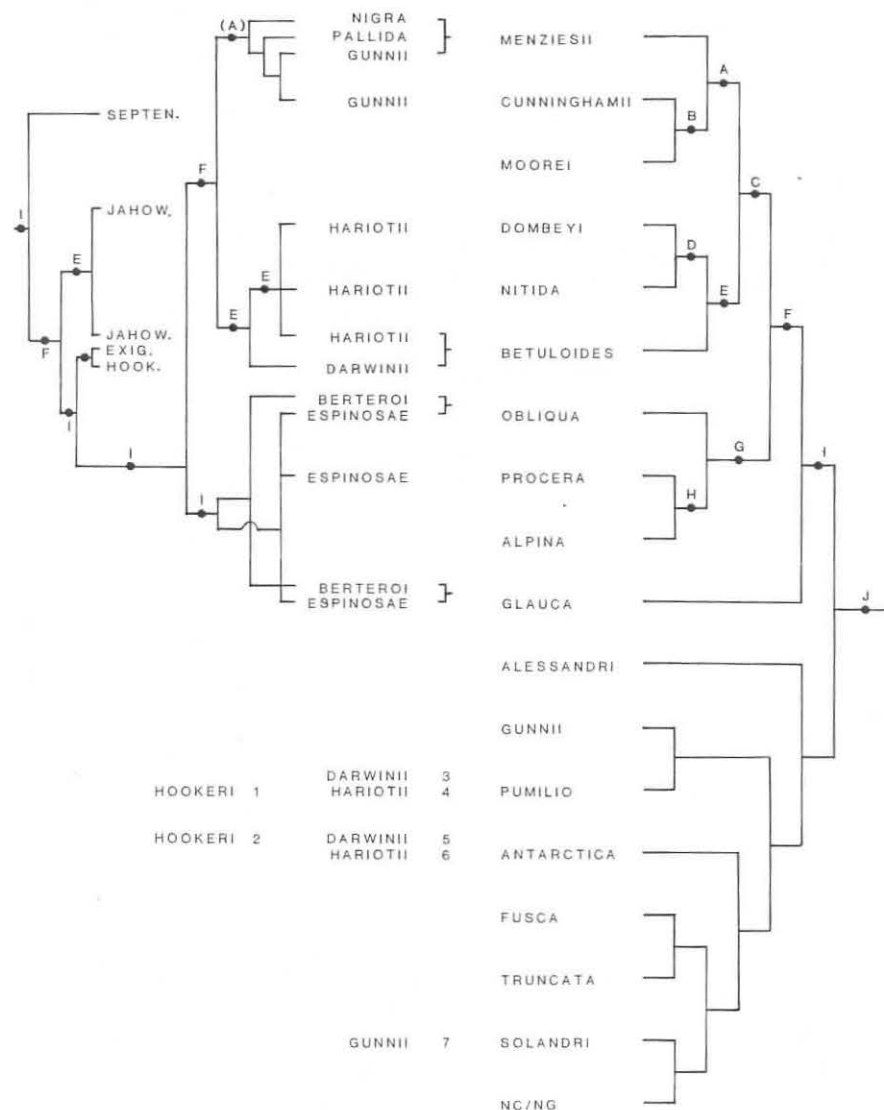


Fig. 4.9. *Cyttaria* cladogram (19) from first analysis (see text) superimposed onto the *Nothofagus* cladogram (Fig. 4.3).

colonizations to three, for two species, and shows only one less obvious component than the *Nothofagus* cladogram.

To have a complete hypothesis that accounts for all of the data in both the *Cyttaria* parasites and their hosts as represented in Fig. 4.10, a sequence resembling that in Fig. 4.11 would be required to account for the 'mismatches'. However, because the distribution of *Cyttaria* in the field

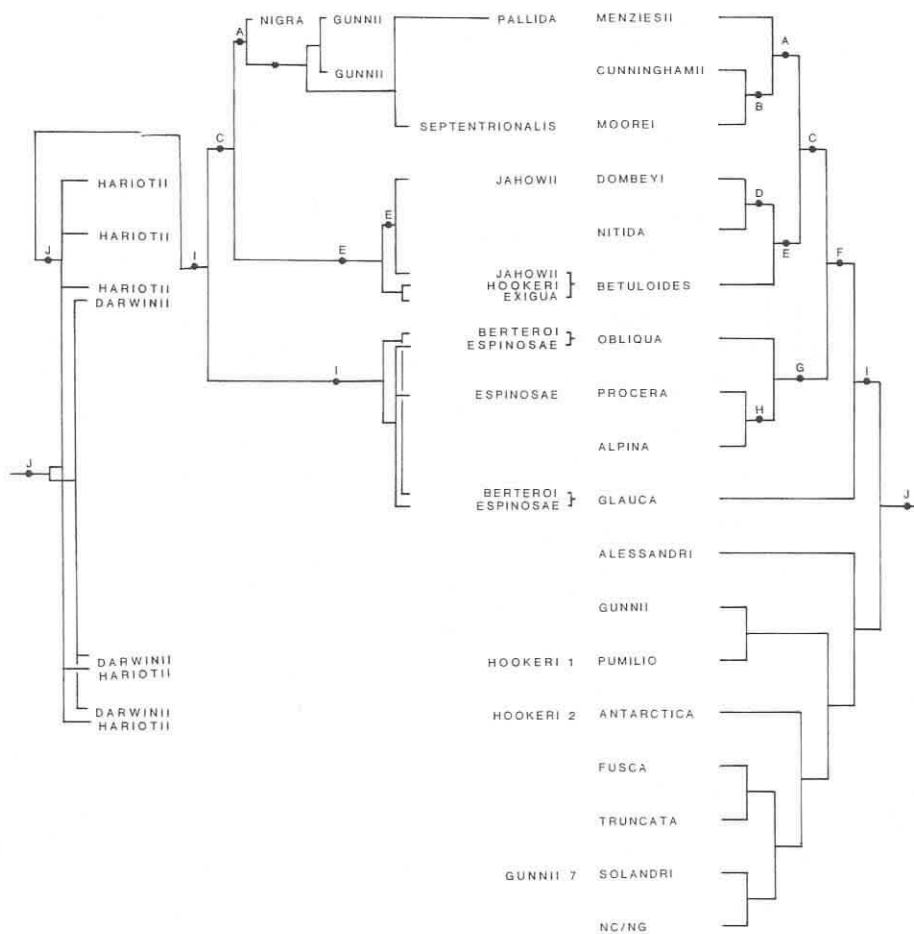


Fig. 4.10. *Cytaria* cladogram (40) from second analysis (see text).

may be poorly known, absence of records of specific parasite-host associations must be interpreted with caution. The speciation of *C. pallida* and *C. septentrionalis* is associated with the phylogeny of *N. menziesii* and the ancestor of *N. cunninghamii* and *N. moorei*. If the *Nothofagus* phylogeny is representative then *C. septentrionalis* failed to invade *N. cunninghamii* in the speciation of this and *N. moorei*. *C. gunnii* is also associated with the speciation of *N. menziesii*, and the ancestor of *N. cunninghamii* and *N. moorei*, but failed to become a parasite of *N. moorei* in the speciation of *N. cunninghamii* and *N. moorei*. To account for the presence of *C. nigra* on *N. menziesii* by an 'association by descent' hypothesis, we have to postulate its presence at the time of speciation of *N. menziesii* and the ancestor of its sister species. Consequently, the only postulate that we

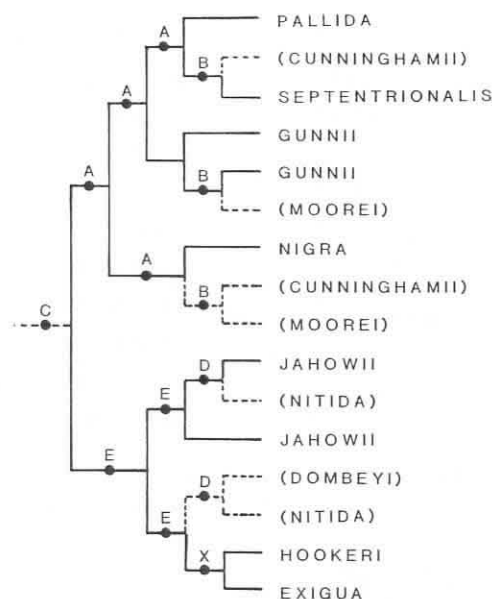


Fig. 4.11. Hypothetical history for *Cyttaria* based on the cladograms in Fig. 4.10. Dotted lines represent those lineages failing to become parasitized or losing parasites (extinction) from the hosts represented at the tips in parentheses. The components common to both host and parasite lineages are indicated by capital letters. X is a unique component of the fungal lineage.

can safely make is that *C. pallida*, *C. nigra*, *C. septentrionalis*, and *C. gunnii* are all associated with the Australasian evergreen species of *Nothofagus*, but only one component 'A' can be ascribed to coevolution. In Fig. 4.11 we have also given a similar scheme for *C. jahowii*, *C. hookeri* and *C. exigua* on the South American species *Nothofagus betuloides*, *N. nitida* and *N. dombeyi*. Here it is important to note that the sister group relation of *C. hookeri* and *C. exigua* implies a speciation event (labelled component X) independent in origin from the phylogeny of *Nothofagus*. By working through the whole phylogeny it has been possible to identify all of the components which can be postulated to be coevolutionary events. In Fig. 4.12 it is clear, as indicated by component 'I', that *Cyttaria espinosa* and *C. berteroi* evolved at the same time as the ancestor for all of the *C. pallida*/*C. exigua* clade. To summarize the maximum number of coevolutionary events we have redrawn Fig. 4.12a in Fig. 4.12b. There are five component nodes common to both *Cyttaria* and *Nothofagus*, labelled A, C, E, I, and J. Component X is an event unique to the fungal group. To assess the extent to which coevolution has occurred we can postulate that speciation was wholly dichotomous. For 11 parasite species there are  $n-1$  or 10 speciation events and thus 5 due to coevolution. Such

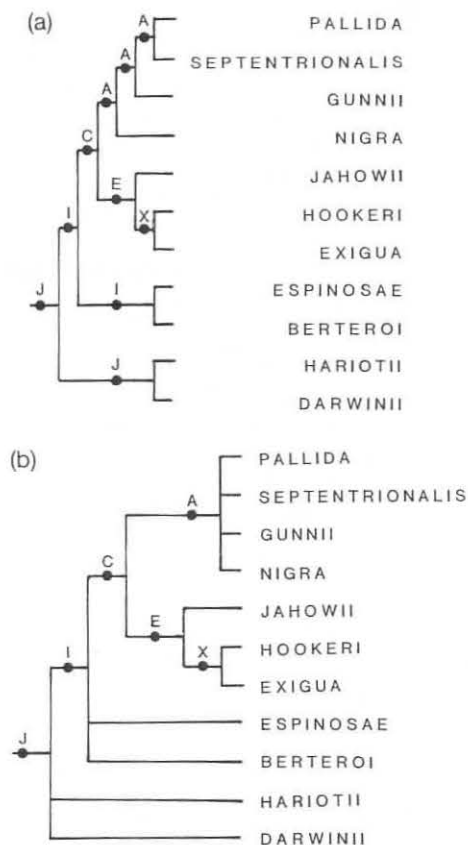


Fig. 4.12(a) Components common to both the *Cyttaria* cladogram and *Nothofagus* cladogram (see Fig. 4.10) expressed on the *Cyttaria* cladogram. (b) Components of cladogram 12a expressed as single events.

an hypothesis, presented in Fig. 4.12b, means that the ancestor of the *C. pallida*/*C. exigua* group, *C. espinosa*, *C. berteroi*, (component I), *C. hariotii*, and *C. darwinii* were all extant at the origin of *Nothofagus*.

A comparison to previous phylogenetic schemes (Fig. 4.13) shows that the hypotheses of Kobayashi and Korf are in agreement on the integrity of the *C. gunnii*/*C. pallida*/*C. nigra*/*C. septentrionalis* group, but vary as to the internal arrangements. The best fit is Kobayashi's phylogeny (Fig. 4.13b) where component 'B' fits the *Nothofagus* phylogeny (Fig. 4.3). Kobayashi's suggestion that at least *C. berteroi* is sister group to the Australasian taxa agrees with our scheme. By contrast, Korf's phylogeny (Fig. 4.13c) places the Australasian taxa as the isolated sister group to all of the remainder, the South American taxa.



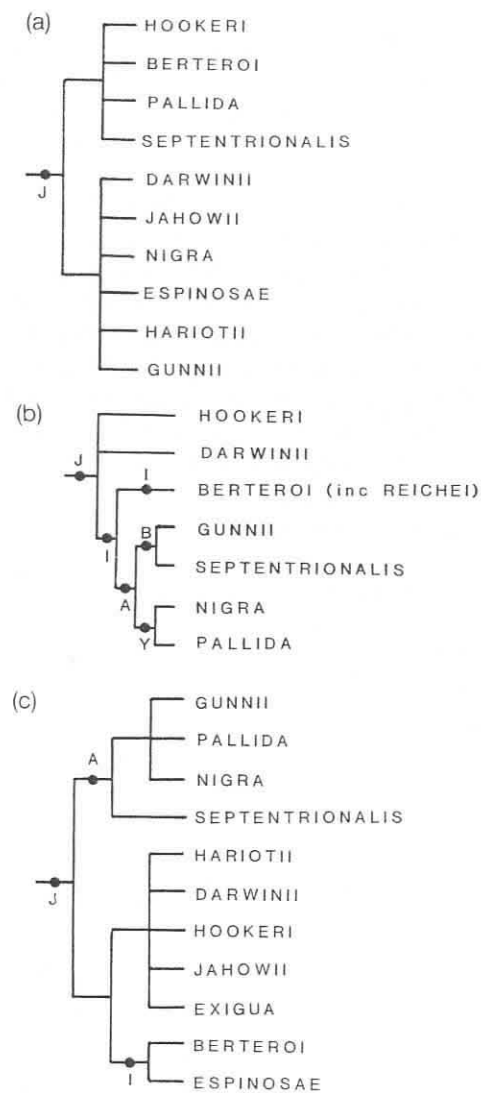


Fig. 4.13. Branching diagrams representing the different phylogenies of *Cyltaria* given by (a) Rawlings (1956), (b) Kobayashi (1966), (c) Korf (1983).

### Historical biogeography

*Nothofagus* has been the subject of intense biogeographic study for the last 100 years or more because it is widely distributed across the southern Pacific Ocean (see Humphries 1981, 1985). By examining the components of the host and parasite phylogenies it should be possible

to examine whether the trans-Pacific disjunctions are common to each of them. *Heterobathmia* occurs only in South America. By substituting areas for the taxa in Figs 4.3, 4.8, and 4.12b and then reducing them to single area statements it is possible to arrive at the area cladograms as given in Fig. 4.14. The *Nothofagus* hosts (Fig. 4.3) have seven area components, as indicated by the nodes in Fig. 4.14. Both the Eriococcidae and *Cyttaria* (Figs 4.8 and 4.12b) have the same two trans-Pacific biogeographic components which are identical to the host patterns (indicated by components A and C). The host taxa and the parasites show an Australasian track that runs between the central eastern part of Australia, north of the Macpherson-Macleay overlap and the southern mountains of Victoria and Tasmania, and into New Zealand, and then a trans-Pacific track to South America (Fig. 4.15). This is entirely separate from the South America/Tasmania track of *N. pumilio* and *N. gunnii* (which is not at all affected by parasites) and the New Zealand/New Guinea/South America track (which is affected by *Cyttaria* only in South America and New Zealand). It seems most likely that the present day disjunct distributions of the parasites and the hosts have shared the same Pacific history. Because *Cyttaria* has possibly two trans-Pacific disjunctions, *Nothofagus* three, and the Eriococcidae one, the groups were well diversified and already present in the early history of the Pacific. Although many commentators have attributed such

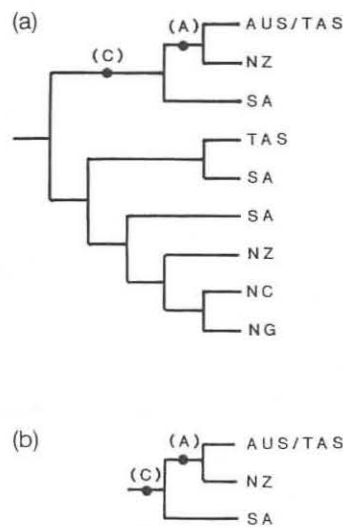


Fig. 4.14. Reduced area cladograms (a) *Nothofagus* (see Fig. 4.3) (b) Eriococcidae (Fig. 4.8) and *Cyttaria* (Fig. 4.12).



Fig. 4.15. Reduced area cladograms from Fig. 4.14a,b expressed as biogeographical tracks.

patterns to the break up of Gondwanaland (see Humphries 1981), Croizat (1964) for example, has repeatedly shown that the New Guinea/Eastern Australia New Caledonia/New Zealand track is a very distinct western Pacific component (see Humphries 1985). Our analyses have shown that in *Nothofagus* and its parasites this track can be subdivided into two sub-tracks linking eastern and southern Australia and Tasmania with New Zealand, and linking New Guinea and New Caledonia with New Zealand. Both of these link a more general Pacific component separately across the southern Pacific to South America. As this pattern is repeated by many groups (see e.g. Croizat 1964) it is most likely to be associated with vicariism in the Pacific rather than an alternative explanation. For references to the speculative geophysical theories that might account for trans-Pacific disjunctions see Humphries and Parenti (1985), and Nur and Ben Avraham (1981).

### Conclusions

(1) To determine patterns of coevolution it is necessary to develop empirical methods that independently assess, but can be equally applied to hosts and parasites.

(2) It is possible only to examine host/parasite interactions in a testable theoretical framework of 'association by descent'. As yet there is no testable theoretical framework to examine parasitism by colonization or host-switching.

(3) Analysis of *Nothofagus* and some of its parasites has shown that coevolution only partially accounts for patterns of relationship and at best 50 per cent, in *Cyttaria* for example. Nevertheless, this is highly significant in such groups.

(4) Coevolved parasites may be as old, if not older than, the group with which they are parasitologically associated. Where they appear older, colonizations from now extinct hosts may have been involved.

(5) At least some components of coevolution are significantly correlated with biogeography. *Nothofagus* and its parasites show corresponding components which are most simply interpreted as vicariance events in Pacific biogeography.

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